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Diversity and composition of arboreal beetle assemblages in tropical pasture afforestations: effects of planting schemes and tree species identity

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Abstract Timber tree plantations are considered for rehabilitating forest biodiversity in the tropics, but knowledge on determinants of faunal diversity patterns in such human-modified forest landscapes is scarce. We quantified the composition of beetle assemblages on three native timber species (*Anacardium excelsum*, *Cedrela odorata* and *Tabebuia rosea*) planted on former pasture to assess effects of tree species identity, tree species diversity, and insecticide treatment on a speciose group of animals in tropical plantations. The beetle assemblage parameters 'abundance', 'species richness', 'Chao1 estimated species richness' and 'Shannon diversity' were significantly reduced by insecticide treatment for each tree species. Shannon diversity increased with stand diversification for *T. rosea* but not for *A. excelsum* and *C. odorata*. Species similarity was highest (lowest species turnover) between beetle assemblages on *T. rosea*, and it was lowest (highest species turnover) for assemblages on insecticide-treated trees of all timber species. Considering trophic guilds, herbivorous beetles dominated on all tree species and in all planting schemes. Herbivores were significantly more dominant on *T. rosea* and *C. odorata* than on *A. excelsum*, suggesting that tree species identity affects beetle guild structure on plantation trees. Insecticide-treated stands harbored less herbivores than untreated stands,

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but exhibited a high abundance of predator beetle species. Our study revealed that even young pasture-afforestations can host diverse beetle assemblages and thus contribute to biodiversity conservation in the tropics. The magnitude of this contribution, however, may strongly depend on management measures and on the selected tree species.

Keywords Canopy arthropods · Community structure · Habitat heterogeneity · Insect diversity · Reforestation · Tourist species

Introduction

Timber harvesting from natural forests and the conversion of forests to pastures and agricultural land act as driving forces for an intensive exploitation and deforestation of tropical forests (FAO 2011; Zahawi 2005 and references therein). This deforestation strongly contributes to loss of global biodiversity and climate change (Houghton 2005; Morris 2010). The establishment of forest plantations that are adapted to local conditions (e.g. by using native tree species) is increasingly viewed as a promising strategy for improving habitat quality and ecosystem functions (Lamb et al. 2005; Paquette and Messier 2010) and for rehabilitating forest biodiversity (Goldman et al. 2008; Harvey et al. 2008; Brockerhoff et al. 2008).

However, to satisfy the demand for forest products (Kelty 2006; Lamb et al. 2005), former plantation forestry, for example in Latin America, primarily concentrated on industrial monoculture tree plantations utilizing fast growing exotic species such as teak (*Tectona grandis*), eucalypts (*Eucalyptus* sp.) or pines (*Pinus* sp.) (Kelty 2006; Park and Wilson 2007). In such plantations, broad-spectrum insecticides are regularly applied to protect trees from herbivore attack (Cunningham et al. 2005; Garen et al. 2009), irrespective of the potential collateral impact on biodiversity. Hence, existent tropical tree plantations may foster landscape homogenization and harbor low biodiversity (Bremer and Farley 2010; Hartley 2002; but see Chey et al. 1998).

Recent research has emphasized that using native instead of exotic tree species planted in mixed stands instead of monocultures may have favorable effects on local biodiversity, as such systems are more closely linked to the local biota and may have more positive effects on local ecosystem processes (Bremer and Farley 2010; Perfecto and Vandermeer 2008; Hartley 2002 and references therein).

However, there is very little empirical evidence that mixed stands of native species harbor greater faunal diversity than monocultures, because most studies do not compare similar sampling units (e.g. plant species per area unit) (Grimbacher et al. 2007). Instead, many authors have estimated animal diversity in secondary versus primary forests, in natural forests versus plantation systems, or in natural forests versus homogeneous agricultural landscapes (e.g. Cunningham et al. 2005; Estrada et al. 1998; Harvey et al. 2006; Philpott et al. 2008; Schulze et al. 2004). Furthermore, empirical studies that assess the effects of insecticide applications on faunal diversity in managed tropical afforestation systems are almost completely lacking.

Beetles are a representative faunal group that can be used to assess effects of management measures on biodiversity within and across spatial units. Arboreal beetles are particularly diverse and well studied (Novotny and Basset 2005; Stork et al. 1997). They belong to different trophic guilds including herbivores, predators and detritivores, contribute greatly to biodiversity in forest habitats, and are involved in ecosystem processes including nutrient fluxes and food web regulation (Erwin 1997; Lassau et al. 2005).

Members of different guilds may show differential responses to environmental characteristics such as tree species composition and individual tree traits (Evans 2001; Price et al. 2011). Accordingly, considering specifically changed environmental characteristics in human-modified landscapes such as tree plantations might lead to testable hypotheses linking species diversity, community ecology and ecosystem functioning (Bascompte 2009; Morris 2010; Tylianakis et al. 2007). In contrast to investigations of beetle assemblages in canopies of natural tropical rainforests (Adis et al. 1984; Davis et al. 1997; Erwin and Scott 1980; Farrell and Erwin 1988), comprehensive studies on arboreal beetle assemblages on native timber trees in tropical plantations are missing yet. However, it would be important to know whether and how plantations alter particular mechanisms governing diversity features compared to natural forest systems (Catterall et al. 2007; Grimbacher et al. 2007). In rainforests, beetle assemblage composition was found to be little influenced by tree species identity when focusing on direct bi-trophic interactions between tree species and beetle assemblages (Wagner 2000). However, beetle assemblage composition differed between tree species when supplementary biotic factors were included such as phylogenetic distance between tree species (Mawdsley and Stork 1997; Novotny et al. 2002), local distances between conspecific tree individuals (Barone 2000), or changing habitat structure (Wagner 2000). These findings support the postulate that the impact of tree species in modified, managed forestry systems on beetle assemblage composition may strongly vary compared to the tree species' impact in natural forests.

In the present study, we investigated the effects of tree species identity and stand diversification on beetle diversity and composition of beetle assemblages on native timber tree species newly established in monocultures and in 3-species mixed stands on former pasture. Insecticide application was used in additional treatments to achieve baseline information on changes in beetle assemblage composition through conventional protection measures. Our specific questions were whether and how (1) tree species identity, (2) tree stand diversification and (3) insecticide application affect beetle abundance, diversity and trophic guild structure on the three native timber tree species *Anacardium excelsum*, *Cedrela odorata* and *Tabebuia rosea* established in an afforestation plantation system.

Materials and methods

Study site and planting design

The study was conducted at an experimental site located in Sardinilla (9°19′30″N, 79°38′00″W), Province Colon, Central Panama. The elevation is around 70 m a.s.l., mean annual precipitation is 2,350 mm, with 25–50 mm per month during the dry season (January–April), and >250 mm per month during the rainy season (May–December) (Plath et al. 2011a). Daily and seasonal temperatures are relatively constant throughout the year, with annual daily maximum temperatures of 33.1 °C and annual mean daily minima of 21.7 °C. The original forest, classified as semideciduous lowland forest and probably similar to the Barro Colorado Island forest (9°9′0″N, 79°51′0″W), was logged in 1952/53. The site was used for agriculture during two years and then converted into pasture by seeding grasses (Scherer-Lorenzen et al. 2007).

The tree species used in this study are *Tabebuia rosea* Bertol. (Bignoniaceae), *Anacardium excelsum* (Bertero and Balb. ex Kunth) Skeels (Anacardiaceae), and *Cedrela odorata* L. (Meliaceae). The three species co-occur in natural Panamanian forest ecosystems (Croat 1978), and are planted to an increasing degree across Central America by

forestry companies and local farmers, because of their suitability for reforestation activities and as valuable timber (ITTO 2006; Wishnie et al. 2007). Potted seedlings of each tree species were raised in a PRORENA (Proyecto de Reforestación con Especies Nativas) nursery for 3 months before being planted on the pasture in August 2006. To support tree establishment, 15 g of 12–72–12 N–P–K granular fertilizer was applied at the time of planting to the bottom of each planting hole and covered with soil before planting, and again 2 months after planting to each seedling on the soil surface. Seedlings of *T. rosea*, *A. excelsum* and *C. odorata* were planted in stands of 36 trees, using a standardized six by six Latin square design with a planting distance of 2 m. Tree individuals were arranged in five planting schemes: (1–3) monocultures for all three timber species, (4) mixed stands comprising the three species (management measure 'stand diversification'), and (5) mixed stands treated with the insecticide/nematicide carbofuran (carbamate, Furadan 10 GR, 5–25 g/tree depending on the effective area of canopy shade) applied to the soil every two months, and by the insecticide cypermethrin (pyrethroid, Arribo EC 20 or 6 EC, 1.2 g/l spray solution) applied to the foliage every 2 weeks after planting (management measure 'insecticide treatment'). The five planting schemes were arranged at one locality, which defined a coherent plot. This plot was replicated five times at different locations across the study site. Concomitant vegetation in the plots was trimmed with machetes to 10 cm height every 3 months during the rainy season (average vegetation height across plots before cutting: 21 ± 5 cm; average tree height across plots at study onset: *T. rosea*: 84 ± 4.9 cm; *A. excelsum*: 55.2 ± 3.7 cm; *C. odorata*: 45.5 ± 3.1 cm; average tree height across plots at the end of the study: *T. rosea*: 201.1 ± 13.0 cm; *A. excelsum*: 120.4 ± 8.3 cm; *C. odorata*: 83.4 ± 6.5 cm).

Insect survey

Insect counts were conducted for all timber trees on a biweekly basis from April 2007 (year 1) to April 2008 (year 2). No survey was conducted at the end of December of year 1 and in the middle of February of year 2. Surveys were conducted as visual census of all insects on a tree's trunk and every leaf during the day and again during the night within a 24 h period. Detected coleopteran individuals were assigned to morphospecies, which were deposited in a reference collection created on the basis of initial survey samplings. Individuals of species sampled for the first time, or individuals not immediately assignable to a morphospecies (hereafter referred to as 'species'), were collected, preserved in 70 % ethanol and allocated to the reference collection. As in tropical regions many taxonomic beetle groups and species remain to be formally described, morphotypes or morphospecies provide a practical solution to deal with previously unrecorded or unidentifiable organisms (Basset et al. 2004; Hammond 1994).

The sequence of planting schemes surveyed within each plot was changed randomly. In untreated and insecticide-treated mixed stands, all 36 trees were sampled (12 individuals per tree species). In the monoculture stands, surveys were carried out on 12 trees for each timber species. The studied tree individuals were randomly selected before starting the insect assessments. To obtain planting positions comparable to the mixed stands, six trees from the edge and six trees from the inner area were investigated each. In the insecticide-treated mixed stands, the biweekly insecticide application was consistently conducted after the biweekly visual insect surveys. In all planting schemes, surveys referred to the same tree individuals for the whole research period. According to this sampling scheme, a total of 540 trees were surveyed at the beginning of the investigation, with 60 trees per species in each of the three planting schemes containing a particular tree species. The number of

surveyed trees declined over the observation period of 12 months as a consequence of tree mortality (*T. rosea* = 1.5 %, *A. excelsum* = 30.4 %, *C. odorata* = 54.1 %). This tree mortality was not affected by planting schemes or herbivore impact, but appeared to be strongly influenced by specific responses of the tree species to the given local site conditions (for details see Plath et al. 2011b). Final analyses included all trees that survived until the end of the sampling period.

Trophic guilds

We distinguished four main trophic guilds following the classification of Stork (1987) as well as Moran and Southwood (1982): (1) herbivores, (2) predators, (3) detritivores, scavengers and fungal feeders, and (4) tourists. The herbivore guild includes species feeding on "higher" live plants. Predators feed on live animals, whereas detritivores, scavengers and fungal feeders (comprised under the name 'detritivores' in the following) feed on dead organic material and fungi. Tourists are non-feeding species that have no intimate or lasting association with the plant during all of their life-stages (Basset et al. 2001; Moran and Southwood 1982). Since tourist species may act as prey of local predators, they were considered as part of the studied beetle assemblages. The assignment of the identified beetle families to the four trophic guilds is given in Table 1.

Data analysis

Beetle abundance (N), species richness (S), Chao1 estimated species richness (S_{Chao1}), and Shannon diversity (D_H) were determined as parameters to describe beetle assemblage composition. Beetle abundance and species richness were calculated as accumulated number of individuals and species, respectively, found in day and night samples for each tree individual and survey event. Singletons were considered as unique singletons (Basset et al. 2008), i.e. species represented by a single individual in the combined data set sampled during the 1-year survey period. We used the Chao1 species richness estimator (for details see Chao 1984; Haddad et al. 2009; Magurran 2004) to estimate the number of beetle species (S_{Chao1}) that can be expected to occur on the studied tree species during the trees' initial growth phase under differing environmental conditions (planting schemes). The Shannon index was converted into a diversity measure using an exponential conversion, following the approach outlined in Jost (2006) (see also Basset et al. 2008).

Effects of planting schemes and tree species identity on beetle assemblage composition were assessed by linear mixed effect models permitting the consideration of multiple nested random effect terms to account for pseudoreplication (Sobek et al. 2009a). Overall effects of planting schemes and tree species identity were assessed using the individual assemblage parameters as response variables (i.e. beetle abundance N, species richness S, Chao1 values S_{Chao1} and Shannon index D_H), planting schemes and tree species as fixed factors, and plot as a random factor, accounting for the nesting of planting schemes within plots and species within planting schemes. The effects of planting schemes on beetle assemblage composition for each focal tree species were assessed using linear mixed effect models with individual assemblage parameters as response variables, planting schemes as fixed factors and plot as a random factor, accounting for the nesting of planting schemes within plots. To account for the potential impact of tree architecture on assemblage parameters, tree height (measured at the end of the growing season in December of year 1) was used as a covariate in each linear mixed effect model. Similarities (species identity) of beetle assemblages were compared between tree species and between planting schemes

Table 1 Overview on the beetle families identified on the three timber species *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata* during the 1-year survey period

	Tabebuia rosea					*Anacardium excelsum*					*Cedrela odorata*				
	N	*S*	S_{rare}	S_{sing}	S_{us}	*N*	*S*	S_{rare}	S_{sing}	S_{us}	*N*	*S*	S_{rare}	S_{sing}	S_{us}
Herbivores															
Apionidae	2	1	1	0	0	4	2	2	1	0	3	2	2	1	0
Attelabidae	2	2	1	0	0	47	1	0	0	0	0	0	0	–	–
Bruchidae	28	7	6	2	2	5	3	3	2	0	7	5	5	3	2
Buprestidae	86	2	1	1	1	7	2	1	1	1	3	1	1	0	0
Chrysomelidae	3,213	74	36	24	16	529	50	36	19	9	461	54	40	22	9
Curculionidae	92	22	7	8	7	90	24	21	13	0	40	15	12	8	2
Elateridae	66	8	4	4	2	6	3	3	2	0	5	5	5	5	1
Scarabaeidae	9	3	2	2	2	18	2	0	0	1	12	1	0	0	0
Detritivores															
Anthicidae	2	2	2	1	1	0	0	–	–	–	3	1	1	0	0
Anthribidae	1	1	1	0	0	2	1	1	0	0	0	0	–	–	–
Cerambycidae	2	2	1	1	0	1	1	1	1	1	0	0	–	–	–
Cucujidae	–	–	–	–	–	1	1	1	1	1	0	0	–	–	–
Endomychidae	4	4	3	1	0	2	2	2	2	1	6	3	3	1	2
Erotylidae	1	1	1	0	0	3	2	2	1	1	0	0	–	–	–
Hydrophilidae	0	0	1	0	0	1	1	1	1	1	0	0	–	–	–
Mycetophagidae	0	0	–	0	0	0	0	–	–	–	1	1	1	–	1
Nitidulidae	1	1	1	1	1	1	1	1	1	1	0	0	–	–	–
Phalacridae	1	1	1	1	1	0	0	–	–	–	0	0	–	–	–
Ptylodactylidae	27	6	3	2	2	7	4	4	1	0	9	3	3	0	0
Sphindidae	1	1	1	1	1	0	0	–	–	–	0	0	–	–	–
Tenebrionidae	10	10	2	1	1	5	3	0	1	1	0	0	–	–	–

Table 1 continued

	Tabebuia rosea					*Anacardium excelsum*					*Cedrela odorata*				
	N	*S*	S_{rare}	S_{sing}	S_{us}	*N*	*S*	S_{rare}	S_{sing}	S_{us}	*N*	*S*	S_{rare}	S_{sing}	S_{us}
Predators															
Cantharidae	287	1	–	–	–	178	1	–	–	–	93	1	–	–	–
Carabidae	27	2	1		–	3	3	3	3	1	6	6	6	6	5
Coccinellidae	78	8	5	2	–	35	3	6	3	2	15	3	1	0	0
Histeridae	1	1	1	1	1	0	0	–	–	–	0	0	–	–	–
Lycidae	26	4	2	1	1	9	2	1	0	0	10	3	2	1	0
Staphylinidae	12	2	–	–	–	19	2	1	1	1	5	2	2	0	0
Trogositidae	1	1	1	1	1	0	0	–	–	–	0	0	–	–	–
Tourists															
Lampyridae	172	3	1	–	–	72	4	0	0	0	99	4	1	–	–
Total	2,464	170	86	55	40	1,045	122	90	54	22	778	109	85	46	22

N number of individuals, *S* number of species, S_{rare} number of rare species (represented with less than five specimens), S_{us} unshared species occurring exclusively on one of the three tree species studied, S_{sing} number of singletons considered as species represented by a single specimen in the combined data set

Families were assigned to the four principal trophic guilds 'herbivores', 'predators', 'detritivores' and 'tourists' following the classification of Stork (1987) as well as Moran and Southwood (1982)

within tree species and between tree individuals within planting schemes using Chao-Sørensen abundance-based similarity index (for details see Chao et al. 2005; Colwell 2009). Assemblage similarities between conspecific tree individuals in the individual planting schemes were compared by Kruskal–Wallis-tests.

The effects of planting schemes and tree species identity on trophic guild structure were assessed by analyses of deviance of the percentage data as well as of the total individual number, with quasi-poisson distribution errors to refit the general linear model (Crawley 2007). For the refitted model, *F*-tests were performed (see also Venables and Ripley 2002). Effects of planting schemes were assessed for each trophic guild within each tree species using one-factorial analyses of deviance with percentage individuals as response variable and planting schemes as between-subject factors. Effect of tree species identity was tested for each trophic guild using percentage individuals as response variable and tree species as between-subject factors.

False discovery rate control, calculating the expected proportion of false-positives among all significant hypotheses with $P < 0.05$, was applied for multiple comparisons following linear mixed effect models, Kruskal–Wallis-tests and analyses of deviance (Garcia 2004; Verhoeven et al. 2005). Variables were transformed as necessary to account for non-normal or heteroscedastic error terms. Species number was square root transformed. Individual number and Chao1 were $\log_{10}(x + 1)$ transformed. Percentage values of the single trophic guilds were arcsin-transformed.

Linear mixed effect models were performed using R 2.13.0 (2011, The R Foundation for Statistical Computing). Sample-based rarefaction curves (Coleman curves), Chao1, Shannon diversity and Chao-Sørensen similarity indices were computed with 50 randomizations using EstimateS (Version 8.2.0, R. K. Colwell, 2009, http://purl.oclc.org/estimates). As EstimateS computes Chao1 and Shannon diversity only for samples where the most abundant species is represented with a minimum of 2 specimens (Colwell 2009), sample numbers (i.e. tree individuals per planting scheme and plot) in estimator analyses differed from analyses on beetle abundance and species richness (for details see Electronic Supplementary Material 1). All remaining statistical analyses were conducted with SPSS 19.0.0 for Mac OS X (2010; IBM SPSS Statistics, Chicago, IL, USA). For clarity, all figures show untransformed data.

Results

Composition of beetle assemblages and related trophic guilds

A total of 5975 beetle individuals belonging to 221 species (morphospecies) in 28 families were collected (Table 1, see also Electronic Supplementary Material ESM 1). Chrysomelidae were the dominating family with 4,203 individuals (70.3 %) followed by Cantharidae and Lampyridae with 558 (15.1 %) and 343 (5.7 %) individuals. Eighty-six species occurred as singletons (38.9 %). The species richness of the collected beetles differed greatly among the families, with more than two-fifths of the species belonging to Chrysomelidae (42.1 %, $n = 93$) and nearly one-fifth belonging to Curculionidae (17.2 %, $n = 38$). Fifty-five beetle species (24.9 % of total species number) occurred exclusively on *T. rosea*, 33 species (14.9 %) on *A. excelsum*, and 22 species (10.0 %) on *C. odorata*.

Herbivores were the most abundant ($n = 4735$, 79.2 %) of the four trophic guilds distinguished in this study, followed by the predators ($n = 805$, 13.5 %) (for details see Table 1). The detritivore and the tourist guilds were represented by relatively few individuals (detritivores: $n = 92$, 1.5 %; tourists: $n = 343$, 5.7 %). Similar to individual

abundance, the herbivores showed the highest absolute species richness ($n = 159$, 71.9 %) of the four trophic guilds, followed by the detritivores ($n = 30$, 13.6 %), the predators ($n = 27$, 12.2 %), and the tourists ($n = 5$, 2.3 %).

Effects of planting schemes and tree species identity on beetle assemblage composition

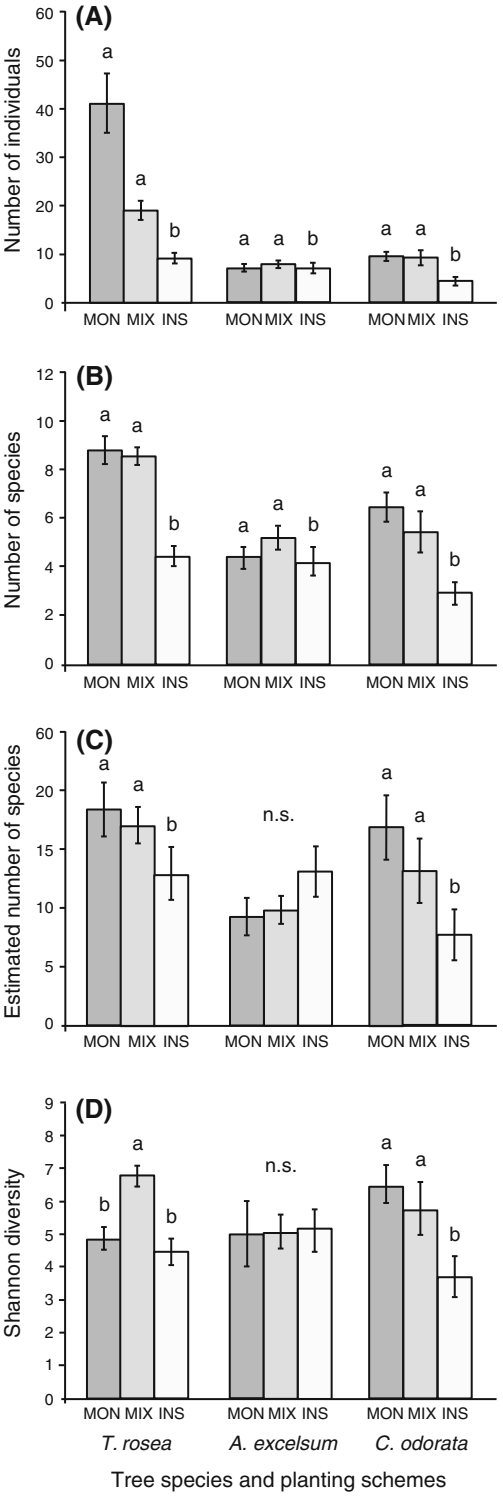
Management measures strongly affected different aspects of beetle assemblage composition in our experimental tree plantation (Table 2). Planting schemes significantly affected overall beetle abundance (*N*: $F_{2,8} = 24.4$, $P < 0.001$), species richness (*S*: $F_{2,8} = 47.0$, $P < 0.001$), Chao1 (S_{Chao1}: $F_{2,8} = 16.8$, $P = 0.001$), as well as Shannon diversity (D_H: $F_{2,8} = 7.6$, $P = 0.014$). Tree species identity, in contrast, had no significant impact on these assemblage parameters ($P > 0.05$ for each response variable). Significant planting scheme × tree species interactions were found for beetle abundance (*N*: $F_{4,24} = 4.75$, $P = 0.006$), species richness (*S*: $F_{4,24} = 4.71$, $P = 0.006$), and for Chao1 (S_{Chao1}: $F_{4,22} = 3.91$, $P = 0.015$), but not for Shannon diversity (D_H: $F_{4,22} = 1.52$, $P = 0.230$).

Intraspecific comparisons of beetle assemblage composition for each focal tree species revealed significant effects of planting schemes (Table 2; Fig. 1), particularly insecticide treatment. For each tree species, mean beetle abundance and mean species richness per tree individual were significantly lower in the insecticide-treated stands compared to untreated monocultures (*T. rosea:* *N*: $P < 0.001$; *S*: $P < 0.001$; *A. excelsum*: *N*: $P = 0.016$,

Table 2 Effects of tree height, tree species identity and planting scheme on beetle assemblage composition described by individual number, observed species number, estimated species number (Chao1 richness estimator) and diversity (Shannon diversity) per tree individual (linear mixed effect model, $P < 0.05$)

Beetle	numDF	denDF	*F*	*P*
Individual number				
Tree height	1	369	164.88	**<0.001**
Species	2	24	3.37	0.051
Planting schemes	2	8	24.39	**<0.001**
Species × planting schemes	4	24	4.75	**0.006**
Species number				
Tree height	1	369	146.21	**<0.001**
Species	2	24	2.27	0.125
Planting schemes	2	8	47.02	**<0.001**
Species × planting schemes	4	24	4.71	**0.006**
Chao1 species number				
Tree height	1	259	57.27	**<0.001**
Species	2	22	2.10	0.147
Planting schemes	2	8	16.84	**0.001**
Species × planting schemes	4	22	3.91	**0.015**
Shannon diversity				
Tree height	1	259	12.83	**<0.001**
Species	2	22	1.51	0.242
Planting schemes	2	8	7.59	**0.014**
Species × planting schemes	4	22	1.52	0.230

Significant *P*-values are given in bold


(A)
Number of individuals
(B)
Number of species
(C)
Estimated number of species
n.s.
(D)
Shannon diversity
n.s.
MON MIX INS
T. rosea
A. excelsum
C. odorata
Tree species and planting schemes

◀ **Fig. 1** Effects of different planting schemes on the beetle assemblages of the three timber species *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata* planted in monocultures (MON) of each tree species, in 3-species mixed stands (MIX), or in 3-species mixed stands treated with insecticides (INS): **A** individual number (N; mean ± SE), **B** species number (S; mean ± SE), **C** estimated species number (S_{Chao1}; mean ± SE) and **D** Shannon diversity (D_H; mean ± SE). *Contrasting small letters* refer to significant differences among planting schemes for each single species (after false discovery rate control of pairwise comparisons; linear mixed effect model, $P < 0.05$). Number of analyzed trees per tree species and planting scheme in (**A**) and (**B**): *T. rosea*: MON = 60, MIX = 60, INS = 59; *A. excelsum*: MON = 57, MIX = 42, INS = 41; *C. odorata*: MON = 44, MIX = 26, INS = 26; number of analyzed trees in (**C**) and (**D**): *T. rosea*: MON = 57, MIX = 57, INS = 35; *A. excelsum*: MON = 38, MIX = 30, INS = 24; *C. odorata*: MON = 31, MIX = 18, INS = 13

S: $P = 0.006$; *C. odorata*: *N*: $P < 0.001$; *S*: $P < 0.001$), as well as compared to untreated mixed stands (for all tree species *N*: $P < 0.01$, *S*: $P < 0.01$) (Fig. 1A, B). Similarly, Chao1 was significantly lower in insecticide-treated stands than in monocultures and untreated mixed stands for both *T. rosea* (S_{Chao1} in monoculture: $P = 0.001$; in mixture: $P < 0.001$) and *C. odorata* (S_{Chao1} in monoculture: $P = 0.002$; in mixture: $P = 0.011$), whereas no such effects were found in *A. excelsum* ($P > 0.05$) (Fig. 1C). Effects of insecticide treatment on Shannon diversity differed across the three tree species. Shannon diversity in treated mixed stands was either significantly lower compared to untreated mixed stands (*T. rosea*, $P = 0.005$), significantly lower compared to both untreated stand types (*C. odorata*, $P \leq 0.001$), or not affected by insecticide treatment (*A. excelsum*, main effect: $P > 0.05$).

Stand diversification significantly affected beetle diversity (D_H) on *T. rosea* (Fig. 1D). Diversity was significantly higher in untreated mixed stands than in monocultures ($P = 0.005$). No effects of stand diversification on other studied assemblage parameters were detected for any of the studied tree species (for each tree species and pairwise comparison $P > 0.05$).

Similarity of beetle assemblages among tree species and planting schemes

Species composition of beetle assemblages on the three tree species was relatively similar, as indicated by Chao-Sørensen similarity values considering the total species pool of each tree species in each planting scheme (*A. excelsum*/*C. odorata* = 0.893, *T. rosea*/*A. excelsum* = 0.946, *T. rosea*/*C. odorata* = 0.975). Comparisons of the individual planting schemes revealed lowest similarities between beetle assemblages on *C. odorata* in insecticide-treated stands and beetle assemblages on *A. excelsum* in monocultures (0.763) and untreated mixed stands (0.785), respectively (Table 3). Highest similarities occurred between beetle assemblages on *T. rosea* in monocultures and *T. rosea* in untreated (0.965) or treated mixed stands (0.952).

Intraspecific comparisons of beetle assemblage similarities between tree individuals within the single planting schemes revealed significant differences for each tree species (Fig. 2; *T. rosea*: $H_{2,5251} = 936.2$, $P < 0.001$; *A. excelsum*: $H_{2,3277} = 113.0$, $P < 0.001$, *C. odorata*: $H_{2,1596} = 152.3$, $P < 0.001$). For all tree species, beetle assemblages among tree individuals within insecticide-treated stands were significantly less similar than beetle assemblages among tree individuals within monocultures (*T. rosea*: $U = 690488.0$, $z = -28.0$, $P < 0.001$; *A. excelsum*: $U = 551744.0$, $z = -6.6$, $P < 0.001$; *C. odorata*: $U = 83894$, $z = -12.3$, $P < 0.001$) or untreated mixed stands (*T. rosea*: $U = 1078378.50$, $z = -14.8$, $P < 0.001$; *A. excelsum*: $U = 245919.0$, $z = -11.0$, $P < 0.001$; *C. odorata*: $U = 32044.0$, $z = -9.07$, $P < 0.001$). Beetle assemblages among tree individuals within

Table 3 Comparisons of species similarity (Chao-Sørensen abundance-based similarity index) of beetle assemblages of the three timber species *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata* planted in monocultures (MON) of each tree species, in 3-species mixed stands (MIX), or in 3-species mixed stands protected by insecticides (INS)

	T. rosea			*A. excelsum*			*C. odorata*		
	MON	MIX	INS	MON	MIX	INS	MON	MIX	INS
T. rosea									
MON	–	0.965	0.952	0.864	0.917	0.913	0.909	0.925	0.870
MIX	–	–	0.911	0.828	0.910	0.910	0.899	0.898	0.801
INS	–	–	–	0.807	0.851	0.838	0.873	0.849	0.843
A. excelsum									
MON	–	–	–	–	0.882	0.857	0.855	0.795	0.763
MIX	–	–	–	–	–	0.850	0.861	0.852	0.785
INS	–	–	–	–	–	–	0.840	0.839	0.796
C. odorata									
MON	–	–	–	–	–	–	–	0.871	0.833
MIX	–	–	–	–	–	–	–	–	0.822
INS	–	–	–	–	–	–	–	–	–

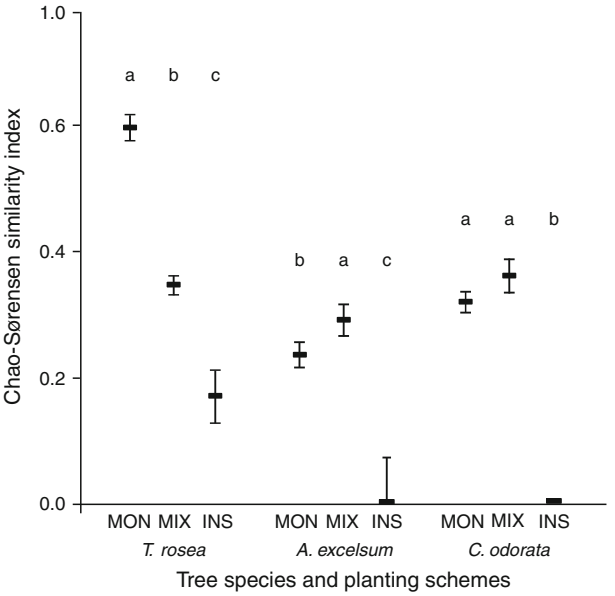


Fig. 2 Effects of different planting schemes on species similarity (median ± 95 % confidence interval) of beetle assemblages of the three timber species *Tabebuia rosea*, *Anacardium excelsum*, and *Cedrela odorata* planted in monocultures (MON) of each tree species, in 3-species mixed stands (MIX), or in 3-species mixed stands treated with insecticides (INS). Contrasting small letters refer to significant differences among planting schemes for each single tree species (after false discovery rate control of pairwise comparisons; Kruskal–Wallis-test, $P < 0.05$). Number of comparisons analyzed within each planting scheme and tree species: *T. rosea*: MON = 1770, MIX = 1770, INS = 1711; *A. excelsum*: MON = 861, MIX = 1596, INS = 820; *C. odorata*: MON = 946, MIX = 325, INS = 325

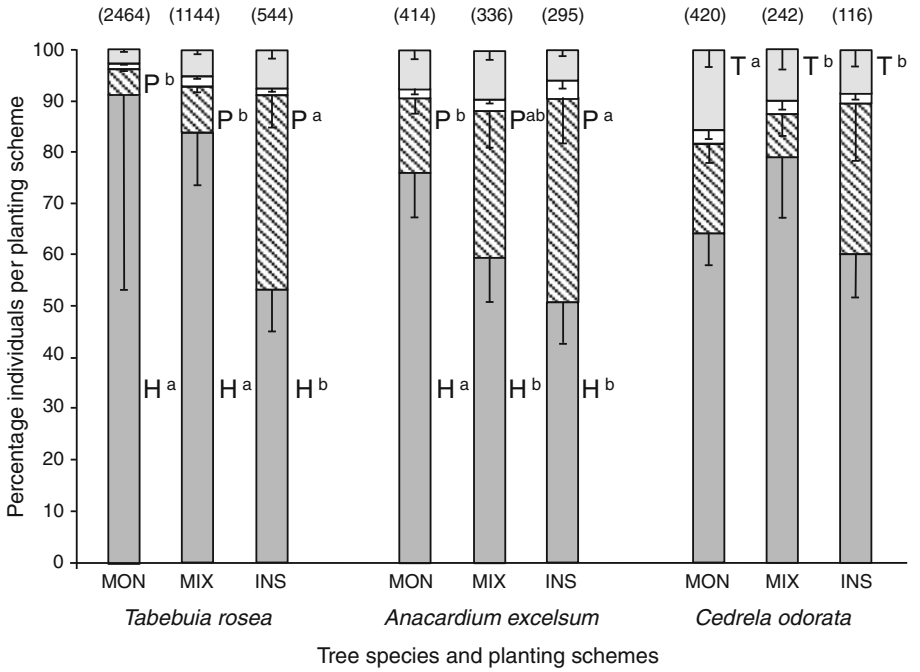


Fig. 3 Percentage of beetle individuals (mean, −SE; absolute beetle number is given in brackets above columns) of the four classified trophic guilds 'herbivores' (H, *dark grey*), 'predators' (P, *shaded*), 'detritivores' (*white*) and 'tourists' (T, *light grey*) per tree individual sampled on the three native timber species *Tabebuia rosea*, *Anacardium excelsum*, and *Cedrela odorata*. Saplings of the timber species were planted in monocultures (MON), in 3-species mixed stands (MIX), or in 3-species mixed stands treated with insecticides (INS). Note that for illustration clarity SE is given only for minus values. *Capital letters* indicate those guilds that differed significantly among planting schemes in intraspecific comparisons; significant differences are given as *small superscript letters* (after false discovery rate control of pairwise comparisons; analysis of deviance, $P < 0.05$). Number of analyzed trees per tree species and planting scheme: *T. rosea*: MON = 60, MIX = 60, INS = 59; *A. excelsum*: MON = 57, MIX = 42, INS = 41; *C. odorata*: MON = 44, MIX = 26, INS = 26

monocultures were significantly more similar than within mixed stands for *T. rosea* ($U = 938730.0$, $z = -20.7$, $P < 0.001$) and less similar for *A. excelsum* ($U = 602096.5$, $z = -5.1$, $P < 0.001$). No differences in similarity were found for untreated stands of *C. odorata* ($P > 0.05$).

Effects of tree species identity and planting schemes on trophic guild structure

Tree species identity significantly affected the contribution of herbivores ($F_{2,412} = 6.8$, $P = 0.001$) and of predators ($F_{2,412} = 4.8$, $P = 0.009$) to beetle guild structure (Fig. 3; Table 4). Herbivores occurred in significantly lower percentages in beetle assemblages on *A. excelsum* (58.8 ± 3.0 %) than in assemblages on *T. rosea* (71.4 ± 2.1 %, $P = 0.002$) or on *C. odorata* (74.0 ± 2.9 %, $P = 0.002$), whereas no differences were found between *T. rosea* and *C. odorata* ($P > 0.05$). In contrast to herbivores, predators occurred in significantly lower percentages in beetle assemblages on *C. odorata* (11.4 ± 2.0 %) than on *A. excelsum* (20.7 ± 2.2 %, $P = 0.003$), whereas no differences were found between

Table 4 Effects of different planting schemes on abundance of beetles of the four trophic guilds 'herbivores', 'predators', 'detritivores' and 'tourists' sampled on the three native timber species *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata*

	T. rosea			*A. excelsum*			*C. odorata*		
	Planting scheme	*F*	*P*	Planting scheme	*F*	*P*	Planting scheme	*F*	*P*
Herbivores	$MON^a > MIX^b, INS^b$	8.91	**<0.001**	$MON^a > MIX^b, INS^b$	4.65	**0.011**	$MON^a, MIX^a > INS^b$	12.01	**<0.001**
Predators	$MON^b, MIX^b < INS^a$	4.68	**0.010**	$MON^b \leq MIX^{ab} \leq INS^a$	5.66	**0.004**	MON^a, MIX^a, INS^a	1.13	0.329
Detritivores	$MON^a, MIX^a > INS^b$	4.45	**0.013**	MON^a, MIX^a, INS^a	0.65	0.524	MON^a, MIX^a, INS^a	1.35	0.264
Tourists	$MON^b, MIX^b < INS^a$	6.49	**0.002**	MON^a, MIX^a, INS^a	0.25	0.780	$MON^a \geq MIX^{ab} \geq INS^b$	4.10	**0.020**

Saplings of the timber species were planted in monocultures (MON), in 3-species mixed stands (MIX), or in 3-species mixed stands treated with insecticides (INS). Contrasting small letters refer to significant differences among planting schemes for each single species (after false discovery rate control of pairwise comparisons; analyses of deviance for count data, quasi-poisson distribution errors, $P < 0.05$). Significant *P*-values are given in bold. Number of analyzed trees per tree species and planting scheme: *T. rosea*: MON = 60, MIX = 60, INS = 59; *A. excelsum*: MON = 57, MIX = 42, INS = 41; *C. odorata*: MON = 44, MIX = 26, INS = 26

T. rosea (16.2 ± 1.6 %) and the two other tree species (for both $P > 0.05$). No differences were found between the tree species for the contribution of the detritivore and the tourist guilds to the beetle assemblages ($P > 0.05$).

Similarly to tree species identity, planting schemes strongly affected the individual beetle guilds within each tree species (Fig. 3). Intraspecific comparisons of beetle guild structure for each tree species revealed significant effects of planting schemes on percentage of herbivorous beetles (on *T. rosea* and *A. excelsum*), of predators (on *T. rosea* and *A. excelsum*) and of tourists (on *C. odorata*) but not of detritivores. Planting schemes also affected the total individual numbers of herbivores (on all three tree species), of predators (on *T. rosea* and *A. excelsum*), tourists (on *C. odorata*) and detritivores (on *T. rosea*) (Table 4).

In beetle assemblages on *T. rosea*, percentage as well as total individual number of either herbivorous beetles and predators strongly differed among the individual planting schemes (percentage: herbivores: $F_{2,176} = 28.3$, $P < 0.001$; predators: $F_{2,176} = 22.7$, $P < 0.001$; total individual number: herbivores: $F_{2,176} = 8.91$, $P < 0.001$; predators: $F_{2,176} = 4.7$, $P = 0.010$). Percentage of herbivores was significantly lower in insecticide-treated stands than in monocultures and in untreated mixed stands (for both comparisons $P < 0.001$). No differences were found for percentage of herbivores between monocultures and untreated mixed stands ($P > 0.05$) (Fig. 3). Total individual number of herbivorous beetles was significantly higher in monocultures than in treated ($P = 0.005$) and in untreated mixed stands ($P = 0.013$) (Table 4). No differences were found for total individual number of herbivores between treated and untreated mixed stands ($P > 0.05$). In contrast to herbivorous beetles, percentage of predators was significantly higher in treated stands than in monocultures and in untreated mixed stands (for both comparisons $P < 0.001$). No differences were found for percentage of predators between monocultures and untreated mixed stands ($P > 0.05$) (Fig. 3). Comparable to percentage values, total individual number of predators was significantly higher in treated stands than in monocultures ($P < 0.001$) and in untreated mixed stands ($P = 0.005$). No differences were found for total individual number of predators between monocultures and untreated mixed stands ($P > 0.05$) (Table 4).

In beetle assemblages on *A. excelsum*, percentage and total individual numbers of herbivorous beetles and predators strongly differed among the individual planting schemes (percentage: herbivores: $F_{2,137} = 10.4$, $P < 0.001$; predators: $F_{2,137} = 4.2$, $P = 0.017$; total individual number: herbivores: $F_{2,137} = 4.7$, $P = 0.011$; predators: $F_{2,137} = 5.7$, $P = 0.004$) (Fig. 3). Percentage of herbivores was significantly higher in monocultures than in untreated and treated mixed stands (for both comparisons $P < 0.001$), whereas no differences in percentage of herbivores were found between untreated and treated mixed stands ($P > 0.05$). Total individual number of herbivores was also significantly higher in monocultures than in untreated ($P = 0.008$) and in treated mixed stands ($P = 0.030$). Whereas no differences were found for percentage of predators between untreated and treated mixed stands ($P > 0.05$), predators contributed less to assemblages in monocultures than in treated mixed stands ($P = 0.008$), but not in untreated mixed stands ($P > 0.05$) (Table 4). Comparable to percentage values, total individual number of predators was lower in monocultures than in treated ($P = 0.002$) but not in untreated mixed stands ($P > 0.05$). No differences in total individual number of predators were found between treated and untreated mixed stands ($P > 0.05$).

In beetle assemblages on *C. odorata*, planting schemes affected the total individual number ($F_{2,93} = 12.01$, $P < 0.001$) but not the percentage ($P > 0.05$) of herbivores in the beetle assemblages (Fig. 2). Total individual numbers of herbivores were significantly

lower in treated than in untreated mixed stands and monocultures (for both comparisons $P < 0.001$). No differences were found between monocultures and untreated mixed stands ($P > 0.05$). Planting schemes also affected the contribution of tourists to beetle assemblages (percentage: tourists: $F_{2,93} = 5.5$, $P = 0.006$; total individual number: herbivores: $F_{2,93} = 4.1$, $P = 0.020$) (Fig. 3). Percentage of tourists was significantly lower in monocultures than in treated ($P = 0.02$) and in untreated mixed stands ($P = 0.016$). No significant differences in the contribution of tourists occurred between treated and untreated mixed stands ($P > 0.05$). In contrast to percentage values, total individual number of tourists was significantly lower in monocultures than in treated ($P = 0.017$) but not in untreated mixed stands ($P > 0.05$).

Discussion

Our study based on a sample size of nearly 6,000 beetle specimens belonging to more than 220 species showed that native timber trees planted on former pasture can host diverse beetle assemblages already 1 year after tree establishment. Furthermore, this investigation demonstrated that conventional pest control by insecticides can strongly reduce beetle species richness as well as beetle diversity and may lead to changes in trophic guild structure of tree-associated beetle assemblages. Interestingly, the predator guild occurred in both higher percentages as well as higher total individual numbers in insecticide-treated mixed stands of *T. rosea* and *A. excelsum* than in untreated monocultures (*T. rosea* and *A. excelsum*) and untreated mixed stands (*T. rosea*). In contrast to insecticide treatments, stand diversification (i.e. 3-species mixed stands) appeared to have relatively weak effects on beetle abundance and species richness on individual young timber trees. As different timber tree species hosted different species and groups of beetles, stand diversification nevertheless contributed to overall-plantation beetle diversity.

Most studies addressing insect diversity and particularly beetle communities in the tropics have focused on rainforest ecosystems, which represent a highly heterogeneous environment with regard to vertical (i.e. stratification of vegetation layers) (Basset et al. 2003 and references therein; Stork et al. 1997) and horizontal (zones of closed forest, gaps, buffer zones, etc.) gradients (Estrada et al. 1998; Grimbacher et al. 2007; Schulze et al. 2004). This heterogeneity is expected to lead to a higher diversity of resources and environmental conditions compared to rather homogenous young forest systems or young tropical afforestations (Hopp et al. 2010; Hartley 2002 and references therein). As studies differ in the methods applied for arthropod sampling (e.g. beating, fogging, pitfall or light traps), comparisons of beetle assemblage composition between studies may be more or less difficult to achieve. Basset (1999) provided one of the first quantitative assessments of the free-living insect herbivores foraging on seedlings in a tropical rainforest based on a sample size of 9,000 specimens and 342 species out of 11 monthly insect surveys on 10,000 tagged seedlings of five common rainforest tree species in Guyana. New (1983) recorded about 4,000 insect herbivores representing 78 species on seedlings of 21 species of *Acacia*. Considering that both studies included several orders of insect herbivores and were conducted on seedlings located in rainforests, the diversity of the beetle assemblages detected in our study on native timber trees in a plantation appears to be comparably high (221 species, 5,975 specimens on 415 tree individuals of three tree species). However, mature secondary forests and older plantations will probably exhibit higher species richness compared to the young afforestation systems evaluated (Hopp et al. 2010; Gormley et al. 2007; but see Barone 2000). Ødegaard (2004), for instance, found 227 beetle species

on only 6 tree individuals of the tree species *Brosium utile* (Moraceae) growing in a tropical wet forest in Panama (average of 84.3 beetle species per tree individual). Erwin and Scott (1980) found even more than 940 species on 19 tree individuals of the neotropical tree species *Luehea seemannii* (Malvaceae) growing in a seasonal forest in the Canal Zone of Panama, which is located nearby our study site. Given that the aforementioned surveys focused on different tree species compared to the timber species selected for the presented study, the differences in alpha-diversity may not only be attributed to a higher heterogeneity of microhabitats in mature forest systems compared to young afforestation systems, but might also reflect an impact of tree species identity on the composition of insect communities (e.g. see Summerville et al. 2003; Vehviläinen et al. 2008).

Effects of tree species identity

Tree species identity appeared to be important for determining beetle species identity in beetle assemblages in our study. Differences in beetle species identity among the tree species indicate that host tree identity may contribute to beetle assemblage composition and thus to local beetle diversity, supporting findings of former studies on assemblages of beetles (Mody et al. 2003; Sobek et al. 2009b), caterpillars (Barbosa et al. 2000; Summerville et al. 2003) or predatory arthropods (Vehviläinen et al. 2008). Furthermore, these differences in beetle species identity among the tree species suggest that the beetle assemblages on the trees were no random samples of beetles from the surrounding vegetation. However, in contrast to beetle species identity, the assemblage parameters beetle abundance, observed and estimated (Chao1) species number, and diversity (Shannon diversity) were not strongly differing among beetle assemblages on the three tree species. These results signify that the three tree species studied hosted beetle assemblages of comparable diversity during their establishment phase. Nevertheless, though tree species identity had only minor impact on beetle alpha diversity, strong planting-scheme × tree species interactions suggest that the effects of stand diversification and insecticide treatment on beetle assemblage composition may strongly depend on the tree species selected for forestry activities.

Effects of stand diversification

Stand diversification increased beetle diversity on one timber species, *T. rosea*, whereas it had no effects on assemblage parameters assessed for beetle assemblages on *A. excelsum* and *C. odorata*. Observations during our census revealed that the effect of stand diversification on Shannon diversity of beetles on *T. rosea* is strongly attributed to a single chrysomelid species, *Walterianella inscripta* Jacoby. This species was found to be the dominant herbivore beetle on *T. rosea*, and it was significantly more abundant in high-density monocultures of *T. rosea* than (a) in mixed-species stands (Plath et al. 2012) or (b) in a silvopastoral system characterized by low densities of *T. rosea* (Riedel et al. 2012). In *A. excelsum* and *C. odorata*, stand diversification was found to have no effect on alpha-diversity of beetles. As the distribution of insect herbivores may be determined by different factors including host plant traits (bottom-up mechanisms) as well as effects of antagonists (top–down mechanisms) (Evans 2001), the missing effect of stand diversification on beetle assemblages in our study is most likely attributed to varying influences of top–down and/or bottom–up mechanisms on the interactions of the individual beetle species with the selected tree species (Koricheva et al. 2006; Ødegaard 2006).

Concerning top–down mechanisms, the natural enemy hypothesis, developed for arthropod assemblages on terrestrial plants, argues that increasing tree stand diversity leads to greater abundances and diversity of natural enemies and an increased effectiveness to reduce herbivore populations (Root 1973). Coleopteran predators, however, showed no differences in their contribution to beetle assemblage composition between monocultures and untreated mixed stands in the present study, indicating that these predators in low-diversity afforestations are not benefiting from a more diverse prey supply through stand diversification. This finding contradicts the natural enemy hypothesis and may add further evidence to recent findings indicating that other factors such as tree species composition rather than tree species diversity affect natural enemies in natural forest systems (Finch 2005; Koricheva et al. 2006; Riihimäki et al. 2005).

Concerning bottom–up mechanisms, increasing plant species richness may increase the number of associated specialized herbivore species ("resource specialization hypothesis"; see Crutsinger et al. (2006) and references therein), which may be reflected in higher overall-plantation species richness. Likewise, if increasing plant species richness may provide more resources and more trophic levels due to higher aboveground net primary productivity, then more herbivore individuals and species will be promoted by increases in accessible energy in more diverse plant stands ("more individuals" hypothesis by Srivastava and Lawton 1998; "species-energy" hypothesis by Wright 1983; "resource diversity" hypothesis by Lawton 1983). Indeed, turn-over rates (as expressed by Chao-Sørensen similarities) of beetle species on *T. rosea* appeared to be higher in mixed stands than in monocultures, which may indicate a higher diversity of resources in the mixed stands due to a comparably more heterogeneous vegetation structure. On the other hand, stand diversification had no significant impact on beetle abundance and species richness in each tree species, contradicting the abovementioned hypothesized bottom-up mechanisms. The finding of a reduced contribution of herbivores to assemblages on *A. excelsum* in the diversified stands compared to monocultures may be explained by a lower attractiveness or suitability to herbivores of *A. excelsum*, which might be more strongly defended than *T. rosea* or *C. odorata* due to relatively high amounts of phenols and tannins (Coley et al. 2002; Dominy et al. 2003). Specialist herbivores may easier overcome strongly expressed defense traits of a plant than generalist herbivores and are therefore assumed to profit from monocultures rather than from mixed plantings (Barbosa et al. 2009; Coley and Barone 1996). Hence the overall percentage of herbivores might be particularly reduced on strongly defended trees growing in tree mixtures as found for *A. excelsum* and associated herbivorous beetle assemblages.

Effects of insecticide treatment

Insecticide application significantly reduced beetle abundance and species richness for each studied tree species. Similarly, it reduced Chao1 and Shannon diversity for beetle assemblages on *T. rosea* and *C. odorata*, emphasizing the detrimental effects of conventional pest control in tropical timber tree plantations on diversity of native insects. Disruptive effects of insecticides on beetle assemblage composition were also suggested by much lower Chao-Sørensen similarities within the insecticide-treated stands compared to untreated stands for all three tree species, indicating a rather unordered re-colonization of treated plots by beetles from adjacent untreated areas. Insecticide application likewise significantly affected beetle guild structure for each focal tree species reducing the percentage of herbivores in treated compared to untreated stands for *T. rosea* and *A. excelsum*. Interestingly, both absolute abundances and percentage of predators (particularly cantharid

beetles) were higher in insecticide-treated stands compared to untreated monocultures in *A. excelsum* or even compared to both monocultures and untreated mixed stands in *T. rosea*. These findings suggest that overall effects of the insecticides used were low on certain predator species, which beyond might experience additional advantage due to insecticide effects on some other species, possibly resulting in decreased interspecific (intra-guild) competition (Szentkirályi and Kozár 1991) and 'interspecific competitor free space' (Plath et al. 2012).

Conclusions

Our study demonstrated that native timber trees in young tropical pasture-afforestations can host comparably speciose beetle assemblages, which may contribute to biodiversity-mediated ecosystem functions in newly established forestry systems. Tree species-specific traits and interactions of the tree species with herbivorous beetles as dominating trophic guild appeared to be important determinants of overall beetle assemblage composition in terms of trophic guild structure and species diversity. By revealing strong negative effects of insecticide treatments on beetle diversity in tropical afforestation systems, our findings emphasize that the development of adequate management strategies for tropical afforestations may contribute to the rehabilitation of local biodiversity. Hence, to enhance the prospects of tropical forest biodiversity, future conservation research should consider tropical afforestation systems allowing a holistic understanding of the relative importance of individual drivers and mechanisms of biodiversity change in a rapidly changing, anthropogenically-modified landscape.

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